Soil organic matter biochemistry and potential susceptibility to climatic change across the forest-tundra ecotone in the Fennoscandian mountains

SOFIE SJÖGERSTEN*, BENJAMIN L. TURNER†, NATHALIE MAHIEU‡, LEO M. CONDRON§ and PHILIP A. WOOKEY*

*Department of Earth Sciences, Uppsala University, Villavägen 16, S-752 36 Uppsala, Sweden, †US Department of Agriculture – Agricultural Research Service, Northwest Irrigation and Soils Research Laboratory, 3793 N 3600 E, Kimberly, Idaho 83341, USA, ‡Department of Chemistry, Queen Mary, University of London, London E1 4NS, UK, §Soil, Plant and Ecological Sciences Division, Lincoln University, PO Box 84, Canterbury, New Zealand

Abstract

We studied soil organic carbon (C) chemistry at the mountain birch forest-tundra ecotone in three regions of the Fennoscandian mountain range with comparable vegetation cover but contrasting degrees of continentality and latitude. The aim of the study was to identify functional compound classes and their relationships to decomposition and spatial variation across the ecotone and latitudinal gradient. Solid-state ^{13}C nuclear magnetic resonance (CPMAS ^{13}C NMR) was used to identify seven functional groups of soil organic C: *alkyls*, *N-alkyls*, *O-alkyls*, *acetals*, *aromatics*, *phenolics* and *carboxyls*. *N-alkyls*, *O-alkyls* and *acetals* are generally considered labile substrates for a large number of saprotrophic fungi and bacteria, whilst *phenolics* and *aromatics* are mainly decomposed by lignolytic organisms and contribute to the formation of soil organic matter together with aliphatic *alkyls* and *carboxyls*. All soils contained a similar proportional distribution of functional groups, although relatively high amounts of *N-alkyls*, *O-alkyls* and *acetals* were present in comparison to earlier published studies, suggesting that large amounts of soil C were potentially vulnerable to microbial degradation. Soil organic matter composition was different at the most southerly site (Dovrefjell, Norway), compared with the two more northerly sites (Abisko, Sweden, and Joatka, Norway), with higher concentrations of *aromatics* and *phenolics*, as well as pronounced differences in *alkyl* concentrations between forest and tundra soils. Clear differences between mountain birch forest and tundra heath soil was noted, with generally higher concentrations of labile carbon present in tundra soils. We conclude that, although mesic soils around the forest-tundra ecotone in Fennoscandia are a potential source of C to the atmosphere in a changing environment, the response is likely to vary between comparable ecosystems in relation to latitude and continentality as well as soil properties especially soil nitrogen content and pH.

Keywords: climate change, CPMAS ^{13}C NMR, decomposition, ecotone, Fennoscandia, soil organic matter

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Introduction

There is currently great interest in the potential impacts of climate change on high latitude soils (boreal forest and

Correspondence: S. Sjögersten, Department of Earth Sciences, Uppsala University, Villavägen 16, S-752 36 Uppsala, Sweden, tel. +14 1330 826336, fax +14 1330 823303, e-mail: sofie.sjogersten@ceh.ac.uk

tundra regions in particular) and the implications of such changes for the global carbon (C) cycle (Robinson & Wookey, 1997; Goulden *et al.*, 1998; Christensen *et al.*, 1999; Hobbie *et al.*, 2000; Oechel *et al.*, 2000). High latitude soils contain large amounts of C (390 Gt under tundra and boreal forest), and there is evidence that even small changes in temperature could enhance decomposer activity and the release of carbon dioxide (CO_2) from

organic matter in these soils (Lloyd & Taylor, 1994; Kirschbaum, 1995). Since climate warming is predicted to be of greater-than-average magnitude at high latitudes, this may have significant feedback implications for global climate change.

The response of high latitude soils to climate warming is likely to depend upon complex interactions between litter inputs, soil properties and microbial decomposition processes, although the precise nature of such interactions remains unclear. One key aspect of the potential response is the C chemistry of the soil organic matter (SOM) and the relative degradation of different functional groups by soil organisms. This will exert a strong control on potential CO_2 release under conditions more favourable for microbial activity (Sjöberg, 2000 (PhD thesis)). For example, most plant-derived carbohydrates are readily degraded in soils (Hopkins *et al.*, 1997), whereas more recalcitrant compounds become stabilised and may persist in the soil for many thousands of years (Wang & Chang, 2001). Chemical information is currently limited for high latitude soils, but detailed information can be obtained using solid-state ^{13}C nuclear magnetic resonance with cross-polarisation magic angle spinning (CPMAS ^{13}C NMR), which has proved a powerful tool in studying the composition and decomposition of SOM (Baldock *et al.*, 1990; Nordén & Berg, 1990; Baldock & Preston, 1995; Kinchesh *et al.*, 1995; Preston, 1996; Baldock *et al.*, 1997; Condron & Newman, 1998; Kögel-Knabner, 2000; Sjöberg, 2000 (PhD thesis); Kögel-Knabner, 2002). The technique provides chemical information on SOM *in situ*, and has clear advantages over conventional procedures, which provide no structural information and involve lengthy and inefficient extraction and fractionation that can alter the compounds under investigation (Schnitzer, 2001). Several functional classes (italics) of soil C are identified by solid-state CPMAS ^{13}C NMR: *N-alkyls* (from proteins), *O-alkyls* (from polysaccharides) and *acetals* (from polysaccharides) are labile substrates to a large number of saprotrophic fungi and bacteria; *phenolics* and *aromatics* (mainly from lignin) require more specialised enzymatic systems and are metabolised mainly at later stages of decomposition by a smaller number of lignolytic organisms (e.g. basidiomycetes) (Hatakka, 1994; Frankland, 1998; Steffen *et al.*, 2000). Aromatic structures in plant material are also found in tannins (polyphenols), which give signals in both the polysaccharide and the *aromatic* chemical shift regions. Paraffinic *alkyl-C*, which is also a major group identifiable by CPMAS ^{13}C NMR, is present in hemi-cellulose and lipids (e.g. cutin and suberin). *Aromatic* structures from lignins and tannins, as well as residues from cutin and suberin, are all important inputs to SOM. *Carboxyl* structures originate from carboxylic acids, but are also formed as products of lignin

transformation (Kögel-Knabner, 1993). For a detailed review that couples the functional groups identified by NMR with the original plant/microbial polymers see Kögel-Knabner (2002).

Most plant-derived compounds are *O-alkyls* (i.e. carbohydrates). The degradation of these and other C compounds increases the concentration of *alkyls*, formed as metabolic products of decomposer organisms and/or through transformation of the original *O-alkyl* structures to more recalcitrant forms (Baldock & Preston, 1995; Hopkins *et al.*, 1997). Plant materials also contain a more recalcitrant carbohydrate fraction, probably associated with lignin (Coûteaux *et al.*, 1998; Huang *et al.*, 1998). Thus, the *alkyl*-to-*O-alkyl* ratio can be used to indicate the degree of decomposition (Baldock *et al.*, 1990; Baldock & Preston, 1995; Baldock *et al.*, 1997; Webster *et al.*, 2000), as can the aromaticity of the SOM (Baldock & Preston, 1995; Baldock *et al.*, 1997).

To understand the potential response of SOM decomposition to environmental warming information is urgently required on the chemical composition and therefore the potential bioavailability of the large pools of C held in high latitude soils. An area that might be particularly sensitive to changes in the environment is the mountain birch forest-tundra ecotone, where shifts in soil C dynamics and soil respiration in relation to above-ground vegetation can occur over short distances (Krosshavn *et al.*, 1992; Raich & Schlesinger, 1992; Körner, 1998; Sjögersten & Wookey, 2002). In fact, vegetation type appears to be more important in determining SOM composition than climatic factors in forest areas in California (Quideau *et al.*, 2001). The forest-tundra ecotone is of particular interest since models of the potential impacts of climate change on high latitude ecosystems predict that large tundra areas will be replaced by boreal woodlands and forest (Emanuel *et al.*, 1985; Kittel *et al.*, 2000; White *et al.*, 2000). Further, palaeoecological evidence suggests that in the early and mid Holocene the mountain birch tree-line was between 300 and 400 m above its present position, largely due to summer temperatures being 1.5–2 °C warmer than today (Barnekow & Sandgren, 2001).

The objectives of this study were (i) to characterise the SOM composition of tundra and mountain birch forest soils in three areas with varying continentality and latitude in the Fennoscandian mountain range, (ii) to detect signals of contrasting rate and pattern in the decomposition processes at these sites and (iii) by reference to parallel studies on soil respiration (Sjögersten & Wookey, 2002) to evaluate the sensitivity of decomposition processes to experimental warming. We adopted an experimental design involving both natural environmental gradients and a warming experiment to address these issues in a short-term experiment.

Materials and methods

Field sites

The three study areas were Dovrefjell (Sør-Tröndelag, Norway), Abisko (Norrbotten, Sweden) and Joatka (Finnmark, Norway) (Fig. 1). These areas form a gradient in both latitude and continentality in the Fennoscandian mountain range; Dovrefjell is the most southerly and maritime, whilst Joatka is the most northerly and continental (Table 1). The study areas are situated in the mountain birch (*B. pubescens* Ehrh. ssp. *czerepanovii* (Orlova) Hämet-Ahti)-tundra ecotone. The main species in the tundra heath areas are *Empetrum hermaphroditum*, *Vaccinium uliginosum*, *V. vitis-idea*, *Betula nana*, lichens and bryophytes (plus *Arctostaphylos uva-ursi* at Dovrefjell). Mesic areas within the mountain birch forest have comparable understorey vegetation, tending towards a greater cover of *V. myrtillus*. The sites are mesic and the soils are predominantly thin spodosols (principally orthods) developed within medium to coarse-grained till deposits (Table 2).

Experimental design

Experimental sites were selected at each research area on both mountain birch forest and tundra heath, subsequently termed forest and tundra, respectively. Ten
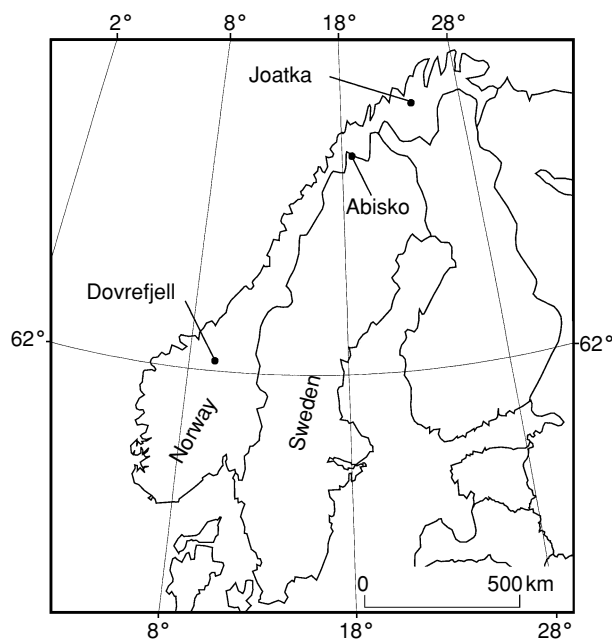
Fig. 1 Map of Scandinavia showing the locations of the main research areas, i.e., Dovrefjell (Norway), Abisko (Sweden) and Joatka (Norway).

Table 1 Environmental information on the three research areas in the Fennoscandian mountains

Area	Location	Elevation (m a.s.1.)	Slope	Temperatures (°C) Minimum	Temperatures (°C) Maximum	Precipitation (mm)	Continentality index (Gorzynski's)[*]	Other information
Dovrefjell	62°18'N, 9°37'E	1000–1100	10° facing NW	−7.9 (Jan.)	10.2 (June)	473	14.4	Alpine tree-line, sharp transition between tundra and birch forest (ca. 50 m). Bedrock in the area is composed of gneisses.
Abisko	68°21'N, 18°49'E	520–600	8° facing NW	−11.9 (Jan.)	11 (June)	304	21.5	Sub-Arctic/alpine tree-line, transition over ca. 3–4 km. Hummocky till deposits, bedrock mainly hard-shale.
Joatka	69°45'N, 23°59'E	420–500	8° facing NE (tundra), SW (forest)	−14.0 (Feb.)	11 (July)	354	24.9	Arctic tree-line, prevailing tundra above 400 m a.s.l., discontinuous birch woodlands. Undulating plateau, precambrian bedrock.

[*]Gorzinski's continentality index $K = 1.7 \times A \times \sin \theta^{-1} - 20.4$ (A = annual temperature range, θ = latitude angle).
[†](Alexandersson et al., 1991).

Table 2 Description of soil profiles at the three areas in the Fennoscandian mountains

Site	Horizon	Depth (cm)	Colour (Munsell)	Texture	pH	Bulk density (g cm^{-3})	Loss on ignition (%)
Dovrefjell							
Tundra	Organic	0–18		Dense, felty	6.18	0.16	88.2
	Oi	0–3					
	Oe	3–12	5 YR 2/3				
	Oa	12–18	5 YR 2/1			0.30	56.5
	Albic	18–32	7.5 YR 4/2	Sand	5.88	1.42	4.63
	Spodic	32–37	7.5 YR 3/3	Gravely sand	6.08		2.88
	C	37–44	2.5 Y 4/3	Silty sand	6.16		
Forest	Organic	0–10	5 YR 3/3	Fibrous/felty	4.46	0.15	68.4
	Oi	0–1					
	Oe	1–7					
	Oa	7–11					
	Albic	11–21	5 Y 5/2	Sandy silt	4.51	1.55	2.13
Abisko							
Tundra	Organic	0–7	7.5 YR 2/3	Felty	3.86	0.14	96.19
	Oi	0–1					
	Oe	1–5					
	Oa	5–7					
	A	7–9	7.5 YR 4/3	Silt	4.35	0.34	50.44
	Albic	9–13	10 YR 5/2	Silt	5.14	0.84	5.62
	Spodic	13–16	10 YR 4/6	Sandy gravel	5.61	1.73	1.014
	C		7.5 YR 3/3	Sandy gravel	6.22	1.66	0.71
Forest	Organic	0–5	5 YR 2/4	Fibrous	5.22	0.066	94.18
	Oi	0–0.2					
	Oe	0.2–4.8					
	Albic	5–8	2.5 YR 5/2	Sandy silt	4.20	1.47	5.18
	C	8–33	2.5 YR 4/3	Silt	5.58	1.10	1.13
Joatka							
Tundra	Organic	0–4	5 YR 2/2	Felty	4.03	0.15	79.8
	Oi	0–0.5					
	Oe	0.5–2					
	Oa	2–4					
	Albic	4–9	10 YR 7/3	Sand	4.85	1.58	0.82
	Spodic	9–22	7.5 YR 4/6	Silty gravely sand	5.13	1.39	2.47
	Iron crust	22–30	2.5 YR 3/3	Gravely sand	5.32	1.44	3.97
	Spodic	30–39	7.5 YR 4/6	Gravely sand	5.89		1.74
	C	39–44		Gravely sand	5.55		
Forest	Organic	0–4	5 YR 2/2	Fibrous	4.07	0.18	78.9
	Oi	0–0.2					
	Oe	0.2–1.2					
	Oa	1.2–4					
	Albic	4–8	10 YR 6/2	Sand	5.30	1.43	1.44
	Spodic	8–28	7.5 YR 5/8	Sand	5.49	1.62	1.03
	C	28–37	2.57Y 5/4	Gravely sand	5.89	1.62	0.86

Two profiles per site were described at Abisko and Joatka. Soil pH was measured in a 1–2 mixture of fresh soil and deionised water.

experimental plots were established at each site, in June 1998. Five 1 m × 1 m plots were designated as controls and five plots were randomly assigned an experimental warming treatment using open top chambers (OTC) (Marion *et al.*, 1997; Hollister & Webber, 2000). Soil temperature data were collected year-round at all three main sites on an hourly basis using TinyTag data-loggers with thermistor probes at 5 cm depth. Soil water content was measured with a ThetaProbe and hand-held ThetaMeter.

Soil sampling and chemical analysis

During July and August 2000 (i.e. after two years of experimental warming), five soil cores (2 cm diameter) were taken from each of the 10 plots at each site. Samples were taken from the organic horizon at two depths where possible (0–2 cm and 2–7 cm), but the organic horizons at Joatka and the forest site at Abisko were generally too thin to allow sampling below 2 cm. Soils were sieved (1 mm), dried (35 °C) and subsamples from each plot (1 g) were combined and mixed thoroughly. Total soil C and nitrogen (N) were determined simultaneously using a Carlo-Erba model NA2000 analyser. Total soil phosphorus (P) was determined by molybdate-reaction following digestion with concentrated sulphuric acid (H_2SO_4), hydrogen peroxide (H_2O_2) and selenium catalyst (Novozamsky et al., 1983). Soil pH was measured in soil-to-deionised water ratios of either 1:2 (soil profile description, Table 2) or 1:10 (soil samples for NMR analysis, Table 3).

Solid-state CPMAS ^{13}C NMR

We acquired CPMAS ^{13}C NMR spectra using a Bruker MSL 300 spectrometer (Bruker Analytik GmbH, Rheinstetten, Germany). The samples were packed into cylindrical zirconia rotors (internal dimension 5.6 mm × 17 mm) sealed with Kel-F caps (3M Company, Minneapolis, MN, USA). We used the following experimental parameters: spectrometer frequency 75.5 MHz, contact time 1 ms, relaxation time 1 s, spinning speed approximately 4.8 kHz, elimination of spinning sidebands using the TOSS (Total Suppression of Sidebands) sequence (Dixon, 1982), and line broadening 50 Hz. We accumulated between 8862 (2.5 h) and 55 826 (15.7 h) scans depending on the C concentration of the soil. Chemical shift values were measured with respect to tetramethylsilane. We used the Bruker WinNMR software to measure peak areas for the following chemical shift regions: 0–47 ppm (alkyl), 47–59 ppm (N-alkyl and methoxy), 59–92 ppm (O-alkyl), 92–112 ppm (acetal),

Table 3 Concentrations of C, N and P and pH in dried soils sampled from control plots and plots that had been experimentally warmed for 2 years using open top chambers (OTC)

Site	Treatment	Depth (cm)	pH	Total C (mg g^{-1} soil)	Total N (mg g^{-1} soil)	Total P (mg g^{-1} soil)	C:N	C:P
Dovrefjell								
Tundra	Control	0–2	4.41	394	16.7	0.96	23.6	412
		2–7	5.17	352	17.4	1.10	20.2	321
	OTC	0–2	5.10	433	17.4	1.00	24.8	435
		2–7	5.04	351	18.5	1.03	18.9	341
Forest	Control	0–2	3.75	400	19.2	1.03	20.9	389
		2–7	nd	420	18.3	0.74	22.9	569
	OTC	0–2	3.74	448	20.6	1.13	21.8	397
		2–7	nd	439	20.3	0.83	21.6	526
Abisko								
Tundra		Litter	3.80	461	11.6	0.90	39.6	510
	Control	0–2	4.14	405	13.3	1.06	30.5	381
		2–7	4.21	385	12.7	0.90	30.3	430
	OTC	0–2	3.71	425	11.8	0.90	36.1	471
		2–7	3.89	429	13.1	0.87	32.8	492
Forest	Control	0–2	3.62	296	14.0	0.91	21.1	326
	OTC	0–2	3.62	330	14.3	0.89	23.0	370
		2–7	3.77	417	18.7	0.83	22.3	500
Joatka								
Tundra	Control	0–2	3.50	427	15.1	1.05	28.4	405
	OTC	0–2	3.50	409	16.5	1.10	24.7	370
Forest	Control	0–2	3.49	370	14.6	0.80	25.3	460
	OTC	0–2	3.49	373	16.0	0.90	23.3	417

Values are single determinations of composite samples from five replicate plots, each of five replicate cores. nd = no data.

112–139 ppm (unsubstituted and *alkyl*-substituted aromatic or aromatic), 139–162 ppm (*O*-substituted aromatic or phenolic), 162–220 ppm (carboxyl, amide, ester, ketone and aldehyde or carboxyl). Actual spectral boundaries were the natural 'valleys' closest to the indicated chemical shift values. The 47–59 ppm chemical shift region is termed *N-alkyl*, but also includes methoxyl-C. As a poorly resolved shoulder on the *O-alkyl* region, the *N-alkyl* region is also prone to over-representation. The contribution of methoxyl-C can be qualitatively assessed by acquiring additional dipolar dephasing (DD) or DD–TOSS spectra, but in the absence of these, it should be remembered that both *N-alkyls* and methoxyls may both contribute to the observed signals in the *N-alkyl* region.

Data analysis

We consider the spectra to be reasonably representative of the total soil C, because C-to-Fe ratios in these soils are ≫1 (Arshad *et al.*, 1988). However, the TOSS procedure may cause some signal loss that is not constant across the spectrum, whilst mobile long-chain C (probably present in poorly decomposed organic layers) may also be undetected by cross-polarisation (Hu *et al.*, 2000). Despite these limitations associated with the quantitative reliability of CPMAS ^{13}C NMR (Preston *et al.*, 1998), we consider it appropriate to use CPMAS ^{13}C NMR to compare intensity distribution and study structural features of soil organic C amongst samples with similar properties (Hopkins *et al.*, 1993; Preston, 1996). Thus, the proportions of the spectral areas assigned to the different functional classes were converted to concentrations in the soil by multiplication with total soil C.

Since we have only single determinations from the five replica plots we analysed the data set using both Principal Component Analysis (PCA) (CANOCO 4.0; Braak & Smilauer, 1998) and analysis of variance (ANOVA) to test for effects of the different areas, depth, warming treatment, and vegetation. Tukey's Honest Significant Difference test was used for means separation. Two separate ANOVA tests were used: one with only the surface sample (0–2 cm), to avoid weighting towards Dovrefjell and Abisko (Joatka lacked 2–7 cm samples), and one with the deeper samples run for Dovrefjell and Abisko only. The PCA was run with both species scaling, which focuses on the separation between the variables, and sample scaling, which displays the actual distance between the samples. We also used multiple regression analysis to test for correlations between total C and the soil chemical composition. Statistical analyses were performed using STATISTICA (StatSoft, 1995). Before running environmental parameters in the PCA the data set was standardised (i.e. zero mean values measured in units of standard deviation).

Results

The chemical composition of the different soils as revealed by CPMAS ^{13}C NMR was generally similar (Fig. 2). Distinct signals were evident within the regions assigned to *alkyls* (31 and 33 ppm), *N-alkyls* (56 ppm), *O-alkyls* (63, 73, 74 and 84 ppm), *acetals* (104 ppm), *aromatics* (115 and 130 ppm), *phenolics* (145 and 153 ppm) and *carboxyls* (174 and 190 ppm). The largest compound class in all soils was *O-alkyls* (117 ± 18 mg g^{-1}; mean ± SD ($n = 19$)); *alkyls* represented the next largest group (82 ± 28 mg g^{-1} ($n = 19$)) followed by similar concentrations of *acetals*, *aromatics*, *N-alkyls*, *phenolics* and *carboxyls* (49 ± 7, 42 ± 8, 40 ± 9, 38 ± 6 and 31 ± 7 mg g^{-1}, respectively ($n = 19$)). No significant correlations existed between the total soil C content and the chemical composition of the samples or the *alkyl*-to-*O-alkyl* ratio.

Statistical analysis (ANOVA) of the top 2 cm of soil revealed several significant differences in chemical composition among sites (Dovrefjell, Abisko and Joatka), and vegetation cover (tundra and mountain birch forest), as well as statistically significant interactions between site and vegetation (Tables 4 and 5). All *P*-values in the text are from the posthoc comparison of means (Tukey's HSD test).

Differences between areas

In general, the SOM at Dovrefjell contained more *acetals*, *aromatics*, *phenolics* and *carboxyls* than Abisko and Joatka ($P < 0.01$ and $P < 0.05$, for *acetals* for Dovrefjell compared with Abisko and Joatka, respectively; $P < 0.01$ and $P < 0.05$ for *aromatics*; $P < 0.001$ and $P < 0.01$ for *phenolics*; and $P < 0.01$ and $P < 0.05$, for *carboxyls*, respectively (Tables 4 and 5)), and the aromaticity was significantly greater compared to Abisko and Joatka ($P < 0.01$ and $P < 0.01$, respectively). Dovrefjell soils also contained lower concentrations of *alkyls* compared to Joatka, although this was marginally not significant ($P = 0.053$). The lowest *alkyl*-to-*O-alkyl* ratio was at Dovrefjell, which was significantly lower than at Abisko and Joatka ($P < 0.01$ and $P < 0.05$, respectively). Proportions of compound classes were similar for Abisko and Joatka. Total C and C-to-N ratios differed significantly between Dovrefjell and Abisko soils ($P < 0.05$; Table 3) with greater total C and lower C-to-N ratios at Dovrefjell. Total N was significantly different at all three areas, with the highest values at Dovrefjell ($P < 0.01$), followed by Joatka ($P < 0.05$) and Abisko ($P < 0.05$). N-to-P ratios were also significantly different between all three areas, with highest values in Dovrefjell ($P < 0.001$) followed by
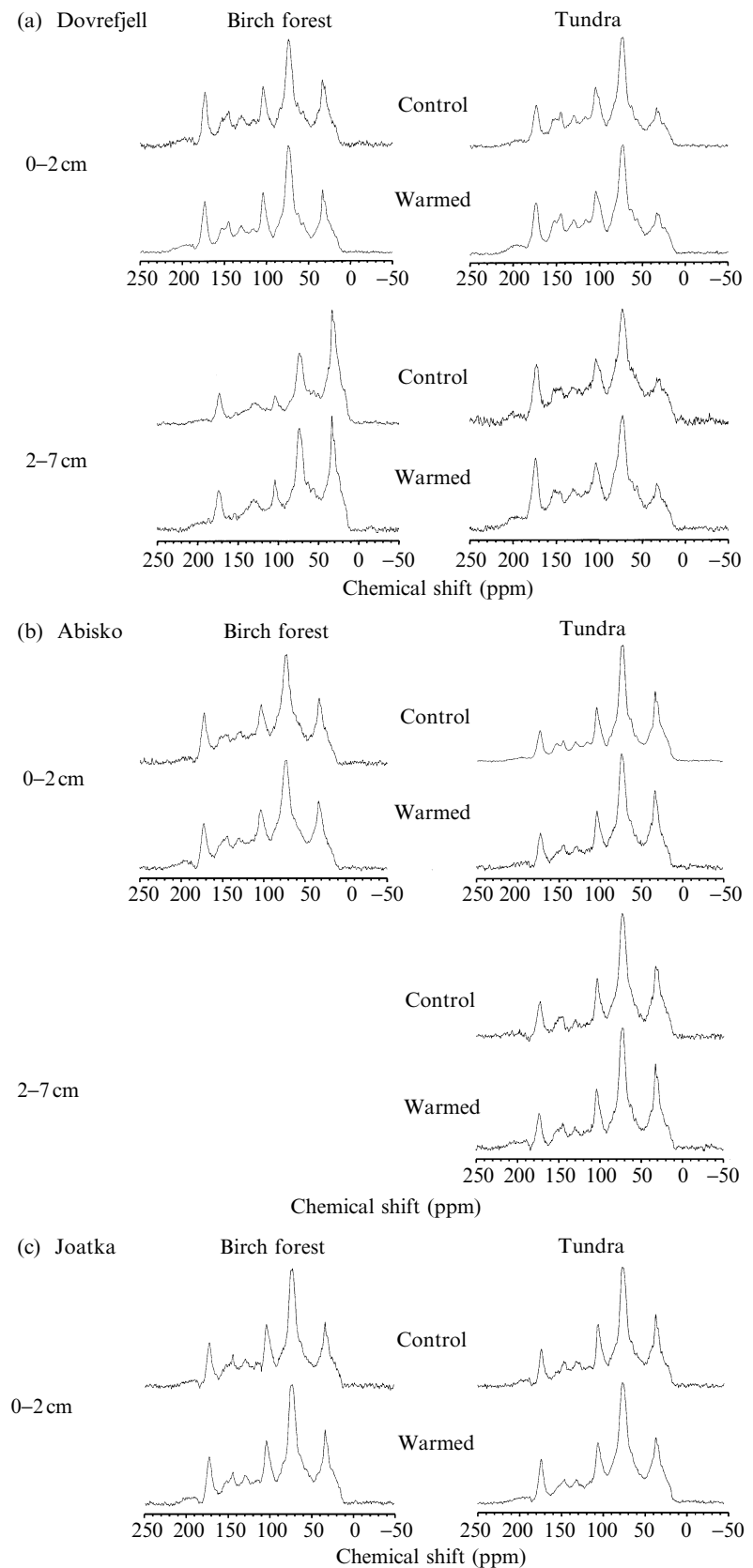
Fig. 2 Solid-state CPMAS ^{13}C NMR spectra of soils at the three field areas (a) Dovrefjell (b) Abisko (c) Joatka. Each sub-diagram shows spectra from forest and tundra soils at 0–2 cm and 2–7 cm depth except at the forest site in Abisko and at the Joatka sites where soils were shallow and allowed no further depths analysis.

Table 4 Concentrations (mg g^{-1} soil) of functional C classes in control and experimentally warmed tundra and forest soils

Site	Treatment	Depth (cm)	Alkyls 0–47 ppm mg g^{-1} soil (% total C)	N-alkyls 47–59 ppm mg g^{-1} soil (% total C)	O-alkyls 59–92 ppm mg g^{-1} soil (% total C)	Acetals 92–112 ppm mg g^{-1} soil (% total C)	Aromatics 112–139 ppm mg g^{-1} soil (% total C)	Phenolics 139–162 ppm mg g^{-1} soil (% total C)	Carboxyls 162–220 ppm mg g^{-1} soil (% total C)	Aromaticity*	Alkyl-to-O-alkyl ratio[†]
Dovrefjell											
Tundra	Control	0–2	52.2 (13.3)	18.4 (4.7)	134.0 (34.0)	57.5 (14.6)	50.1 (12.7)	40.9 (10.4)	40.7 (10.3)	0.23	0.25
		2–7	52.3 (14.9)	23.4 (6.7)	108.3 (30.8)	50.1 (14.2)	42.0 (11.9)	34.1 (9.7)	41.1 (11.7)	0.22	0.29
	OTC	0–2	59.6 (13.8)	22.7 (5.2)	135.3 (31.3)	60.7 (14.0)	55.7 (12.9)	47.0 (10.8)	52.7 (12.2)	0.24	0.27
		2–7	43.3 (12.3)	21.8 (6.2)	101.6 (29.0)	47.6 (13.6)	47.3 (13.5)	35.8 (10.2)	53.5 (15.3)	0.24	0.25
Forest	Control	0–2	76.8 (19.2)	25.0 (6.2)	117.5 (29.4)	51.0 (12.7)	47.4 (11.9)	36.5 (9.1)	45.7 (11.4)	0.21	0.40
		2–7	158.2 (37.7)	32.7 (7.8)	105.2 (25.0)	28.9 (6.9)	41.9 (10.0)	20.2 (4.8)	32.9 (7.8)	0.15	0.95
	OTC	0–2	81.4 (18.2)	22.1 (4.9)	144.4 (32.2)	53.7 (12.0)	51.6 (11.5)	40.2 (9.0)	54.3 (12.1)	0.20	0.37
		2–7	120.2 (27.4)	33.7 (7.7)	123.3 (28.1)	12.9 (9.8)	53.1 (12.1)	21.4 (4.9)	44.5 (10.1)	0.17	0.60
Abisko											
Tundra		Litter	94.6 (20.5)	25.4 (5.5)	159.1 (34.5)	55.1 (12.0)	51.0 (11.1)	33.9 (7.4)	41.8 (9.1)	0.18	0.40
	Control	0–2	91.8 (22.7)	19.3 (4.8)	151.1 (37.3)	48.9 (12.1)	35.7 (8.8)	27.6 (6.8)	30.6 (7.6)	0.16	0.42
		2–7	91.0 (23.6)	21.8 (5.7)	150.2 (39.0)	47.7 (12.4)	23.9 (6.2)	21.0 (5.4)	29.4 (7.6)	0.12	0.41
	OTC	0–2	97.6 (23.0)	24.3 (5.7)	154.2 (36.3)	52.1 (12.3)	35.4 (8.4)	26.8 (6.3)	34.7 (8.2)	0.15	0.42
		2–7	102.1 (23.8)	21.6 (5.0)	152.0 (35.4)	52.1 (12.2)	34.6 (8.1)	28.8 (6.7)	37.7 (8.8)	0.15	0.45
Forest	Control	0–2	52.2 (17.6)	20.9 (7.1)	95.0 (32.1)	35.4 (12.0)	38.9 (13.1)	23.4 (7.9)	30.3 (10.2)	0.21	0.35
	OTC	0–2	62.4 (18.9)	19.0 (5.8)	108.5 (32.9)	42.7 (12.9)	36.4 (11.0)	28.3 (8.6)	32.7 (9.9)	0.20	0.37
Joatka											
Tundra	Control	0–2	88.9 (20.8)	26.9 (6.3)	149.4 (35.0)	52.0 (12.2)	44.8 (10.5)	28.0 (6.6)	37.4 (8.8)	0.17	0.39
	OTC	0–2	84.3 (20.6)	26.7 (6.5)	149.9 (36.7)	50.9 (12.4)	34.1 (8.3)	26.1 (6.4)	36.9 (9.0)	0.15	0.37
Forest	Control	0–2	65.9 (17.8)	23.0 (6.2)	125.3 (33.9)	45.1 (12.2)	42.6 (11.5)	29.5 (8.0)	38.0 (10.3)	0.20	0.34
	OTC	0–2	74.6 (20.0)	19.9 (5.3)	126.2 (33.8)	47.8 (12.8)	40.0 (10.7)	28.1 (7.5)	36.3 (9.7)	0.18	0.38

Values are single determinations of composite samples from five replicate plots, each of five replicate cores. Values in parenthesis are the proportion (%) of the total C.
*Calculated as total aromatics (*aromatics + phenolics*)/total signal from all compounds.
[†]Calculated as *alkyls/(N-alkyls + O-alkyls + acetals)*.

Table 5 Summary output of ANOVA for the ^{13}C NMR CPMAS data

Compound	Effect	df	F	P
Alkyls	Area	2	4.9	0.052
	Vegetation	1	11.5	*
	Area × vegetation	2	35.0	***
N-alkyls	Area	2	1.4	ns
	Vegetation	1	1.0	ns
	Area × vegetation	2	3.2	ns
O-alkyls	Area	2	1.4	ns
	Vegetation	1	27.0	**
	Area × vegetation	2	7.4	*
Acetals	Area	2	16.4	**
	Vegetation	1	23.9	**
	Area × vegetation	2	1.5	ns
Aromatics	Area	2	15.8	**
	Vegetation	1	0.0	ns
	Area × vegetation	2	0.7	ns
Phenolics	Area	2	38.7	***
	Vegetation	1	1.4	ns
	Area × vegetation	2	2.0	ns
Carboxyls	Area	2	13.6	**
	Vegetation	1	0.1	ns
	Area × vegetation	2	0.3	ns
Alkyl-to-O-alkyls	Area	2	14.0	**
	Vegetation	1	1.6	ns
	Area × vegetation	2	28.0	**
Aromaticity	Area	2	31.0	**
	Vegetation	1	11.4	*
	Area × vegetation	2	18.6	**

Main effects are shown, together with factorial interactions. Statistical significance of comparisons is reported as P-values, denoted by: *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, ns = not significant.

Joatka ($P < 0.001$) and Abisko ($P < 0.001$). C-to-P ratios in soils from all areas were similar.

Depth distribution

Total C contents showed no consistent depth distribution, but C-to-N ratios decreased with depth at six of the seven sites where sampling at 2–7 cm was possible (Table 3). At Dovrefjell and Abisko a near-significant decrease of the concentrations of *aromatics* ($F = 4.0$, $P = 0.073$) and *phenolics* ($F = 4.8$, $P = 0.052$) with depth was noted, although, for *phenolics* a significant ($F = 4.9$, $P < 0.05$) interaction between area and depth indicate that the variation in concentration of *phenolics* with depth is only present at Dovrefjell. In four of six soils *alkyl*-to-*O-alkyl* ratio increased with depth, and aromaticity decreased with depth, however, this was not statistically significant.

Differences between vegetation types (tundra vs forest)

Significantly higher concentrations of *alkyls* ($P < 0.05$), *O-alkyls* ($P < 0.01$) and *acetals* ($P < 0.01$) were found in tundra compared to forest, as well as lower aromaticity ($P < 0.05$) in tundra soils. Tundra soils also contained greater amounts of total C ($P < 0.05$), higher C-to-N ratios ($P < 0.01$) and lower N-to-P ratios ($P < 0.01$). Significant interactions between area and vegetation were observed for *alkyls*, *O-alkyls* and, consequently, for the *alkyl*-to-*O-alkyl* ratios and aromaticity. In tundra soils at Dovrefjell both the concentration of *alkyls* ($P < 0.01$) and the *alkyl*-to-*O-alkyl* ratio ($P < 0.01$) were significantly lower compared to tundra soils at Abisko and Joatka. Further, significantly higher aromaticity was found in tundra soils in Dovrefjell compared to tundra soils at Abisko ($P < 0.01$) and Joatka ($P < 0.01$). For *O-alkyls* the forest soil in Abisko was the only forest site with significantly or near significantly ($P = 0.063$, $P < 0.01$, $P < 0.05$; at Dovrefjell, Abisko and Joatka, respectively) lower concentrations compared to tundra soils. This was also the case for total C ($P < 0.05$), where the forest site in Abisko influenced the significant difference between forest and tundra soils.

A more complex pattern was evident when the 2–7 cm depth samples were included in the analysis. PCA analysis revealed that *alkyls*, *N-alkyls* and *O-alkyls* were negatively correlated with the *aromatic*, *carboxyl*, *phenolic* and *acetals* on the first ordination axis (Fig. 3a); the first and second principal component explained 88% of the variance. The first component separates Abisko and Joatka tundra soils on the right from the forest soils on the left (Fig. 3b). The Dovrefjell tundra soils group to the left whilst the forest soils from that site are not closely grouped. The separation of the first principal component axis is mainly controlled by the concentrations of *alkyls* (Eigenvalue (EV) = 1.89) followed by *O-alkyls* (EV = 0.63) and *phenolics* (EV = −0.28). This implies higher concentrations of *alkyls* and *O-alkyls* in the soil samples to the right in Fig. 3b and higher concentrations of *phenolics* to the left. The second principal component axis is dominated by the *O-alkyls* (EV = −1.28) and *acetals* (EV = −0.45) and separates most of the forest soils (top half of Fig. 3b) from tundra soils (lower half of Fig. 3b) (i.e. higher concentrations of *O-alkyls* and *acetals* in tundra soils).

Correlations between environmental variables and chemical composition of the SOM

An attempt was made to evaluate relationships between SOM composition determined by CPMAS ^{13}C NMR and environmental parameters using PCA ordination (Fig. 4). Interpretation was limited because standardisation of the data may have created bias, but some
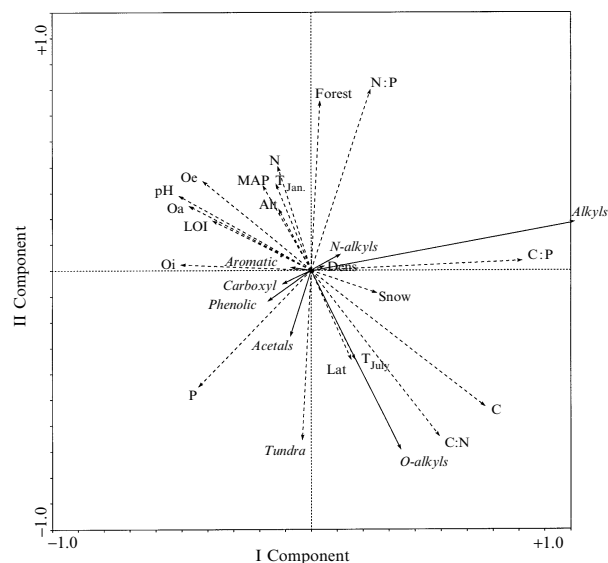
(a)

(b)

○ Control ● Warmed
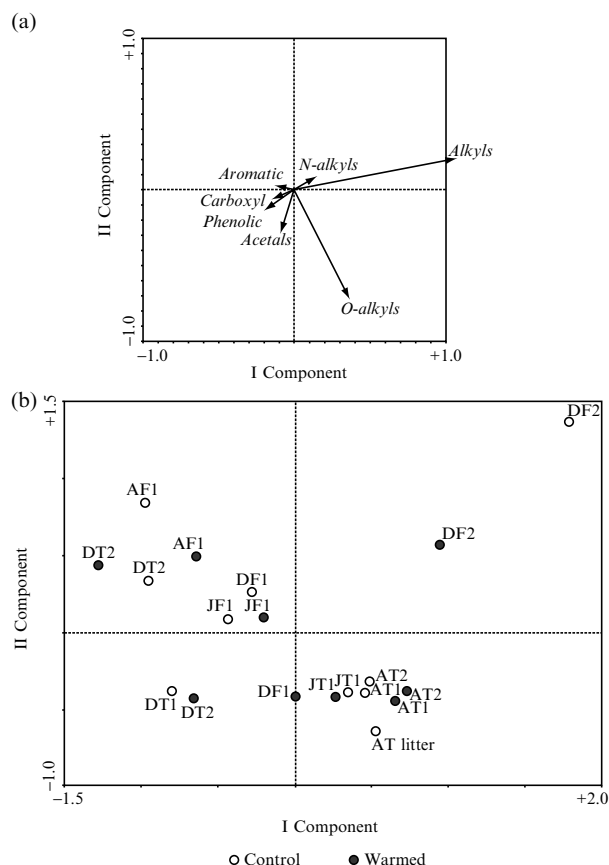
Fig. 3 Principal components analysis showing the grouping of soil samples in response to vectors describing the chemical composition. The analysis was run both (a) species-scaled (i.e. the focus on the chemical compound vectors), and (b) sample-scaled (i.e. the scaling showing the actual intersample distances) to facilitate separation and grouping of samples. D (Dovrefjell), A (Abisko), J (Joatka); F (Forest), T (Tundra); 1 (0–2 cm), 2 (2–7 cm).

Fig. 4 Correlation between standardised environmental parameters (······) and chemical compounds (——). The model was indirect linear (PCA) interpreting correlation from all variance, with the following environmental parameters: Oi (depth of the litter layer (cm)), Oe (depth of the humic layer (cm)), Oa (depth of the humus layer (cm)), dens (density $(g\,m^{-3})$), pH, LOI (loss on ignition), C (total carbon $(mg\,g^{-1})$), N (total nitrogen $(mg\,g^{-1})$), P (total phosphorous $(mg\,g^{-1})$), C:N, C:P, N:P, tundra, forest, lat (latitude), alt (altitude), snow (duration of snow cover (days)), MAP (mean annual precipitation (mm)), T_{Jan} (January mean temperature (°C)), T_{July} (July mean temperature (°C)).

interesting relationships emerged. Concentrations of *O-alkyls*, for example, were positively correlated with C:N and negatively correlated with total N, and the *alkyl* vector was positively correlated with C:P. Further, the depth of the organic horizons was positively correlated with pH.

Experimental warming

The OTCs generally decreased soil moisture content and increased surface temperature at all sites (1–2 °C based on the July average), but soil temperature at 5 cm was not significantly affected (Table 6). The effect of the OTCs on surface temperature was clearest at tundra sites. After 2 years of warming no significant change in C, N or P content, or C chemistry, was detected in either the 0–2 cm or 2–7 cm layers at any of the sites.

Discussion

Organic matter in the subalpine and subarctic soils of the Fennoscandian mountains contains similar proportional distributions of functional C groups as soils from a wide range of climates and land uses, including tropical, temperate and agricultural soils, with a wide range of organic matter contents and physical properties (Mahieu *et al.*, 1999). Indeed, soils throughout the world appear to contain the same distribution of functional C groups irrespective of pedogenesis, climate, vegetation and management regimes. Thus, total *O-alkyls* are the dominant functional class, followed by *alkyls*, total aromatics and carbonyls. The soils of the current study contain a substantial proportion of *O-alkyls*; approximately 52% compared to the range of values for 311 whole soils (35–55%) (Mahieu *et al.*, 1999), despite the cold environment and the generally poor litter quality (woody, and lignin rich). The general agreement of compound distribution, despite highly variable C content and environmental setting, suggests that SOM is degraded by similar pathways, with the rate of decomposition being mainly controlled by litter quality and the physical environment, but with the

Table 6 Temperature (unshielded surface temperatures and soil temperatures at 5 cm depth) and soil moisture data for control and OTC plots at tundra and forest sites at all study areas

	Dovrefjell				Abisko				Joatka			
	Control		OTC		Control		OTC		Control		OTC	
	Tundra	Forest	Tundra	Forest	Tundra	Forest	Tundra	Forest	Tundra	Forest	Tundra	Forest
Annual T surface (°C)	1.1	2.9	2.4	3.0	0.8	2.2	2.1	nd	1.0	2.4	2.2	2.2
July T surface (°C)	9.5	10.6	11.1	10.2	12.9	12.6	13.7	nd	14.3	14.2	16.8	15.4
Annual soil T (°C)	1.4	nd	1.3	nd	0.9	2.3	nd	nd	nd	1.7	nd	1.9
July soil T (°C)	6.5	11.5	6.9	7.6	8.3	9.9	nd	nd	11.5	9.9	nd	10.8
Soil moisture content ($m^3H_2OM^{-3}$ soil)	0.30	0.36	0.27	0.30	0.33	0.26	0.30	0.28	0.19	0.20	0.13	0.18

Temperature data was collected on an hourly basis and data presented here are average values (yearly and July) for 2000. Soil moisture was collected less frequently and only from June to September. For soil moisture content measurement at Dovrefjell, Abisko and Joatka, $n = 6$, $n = 6$, $n = 1$, respectively. nd = no data.

same end-products of the process (Jenkinson & Ayanaba, 1977). Thus, in a long-term (23 years) decomposition experiment on a subarctic bog, different litter material resulted in similar amounts of residual material despite large differences in initial litter chemistry and decomposition rates (Latter et al., 1998).

Despite the similarity of the C chemistry of our soils with the general global pattern we found some significant finer scale differences between contrasting areas and vegetation types. For example, clear differences in C chemistry were apparent amongst sites along the ca. 8° latitudinal gradient represented here. Whether this is related to latitudinal differences in the input of organic matter to the soil, contrasting decomposition pathways, or a combination of the two, remains unclear. However, we speculate that the contrasts in C chemistry between the studied regions and vegetation types might be related to soil N availability and that the response of soil C to a climate warming would be strongly modulated by soil N content. This hypothesis is supported by the greater C accumulation and higher concentrations of aromatic compounds at Dovrefjell (i.e. the area with the most favourable climate for biological activity), which may be a response to a greater degree of humus formation in these less acidic soils with greater N contents (Berg et al., 1996; Magill & Aber, 1998; Berg, 2000; Prescott et al., 2000; Thomas & Prescott, 2000).

We conclude that vegetation cover (i.e. mountain birch forest compared to tundra heath) greatly influences soil C dynamics, with, for example, greater C accumulation in tundra soils and contrasting degrees of decomposition. Clear differences between forest and tundra soils were detected, with accumulation of labile carbon in the surface layer of tundra soils. The *alkyl*-to-*O-alkyl* ratio was also lower in tundra soils, indicating less decomposed

organic material. Clear differences in soil respiration and litter decomposition (measured during 4 years; S. Sjögersten, unpublished data) were detected between forest and tundra soils from these sites, with markedly higher decomposition rates in soils under birch forest (Sjögersten & Wookey, 2002). For example, at Abisko ca. 30% higher soil respiration rates were measured from forest soils compared to tundra. The difference in SOM composition might be due to the litter input (Quideau et al., 2001), but the results from parallel studies (Sjögersten & Wookey, 2002; S. Sjögersten, unpublished data) indicate that the more sheltered microclimate within the mountain birch forest increases decomposition rates. [14]C accelerator mass spectrometry (AMS) dating of both soil macrofossils and bulk material from the forest and tundra sites at Abisko indicates generally older material in forest soils compared to tundra (200 and 50 years, mean residence time, respectively, at the base of the organic horizon) (P. Thermaenius, 2001, pers. comm.). This suggests that a higher degree of soil stabilisation occurs within the forest and that SOM at tundra sites contains a larger proportion of unstable poorly decomposed material. The SOM stabilisation probably results from the more favourable microclimate within the forest, and may be linked with greater N contents in forest soils compared to tundra (as discussed above). The impact of the above ground vegetation community on SOM composition suggests that shifts in the tree-line in these regions in response to climate change have the potential to alter substantially soil C dynamics.

The noted contrasts in soil C chemistry along the latitudinal gradient and between forest and tundra vegetation suggest that both regional- and microclimate are of significance to SOM dynamics. This probably involves both direct impacts of climate on decomposition rates,

plus more complex interactions between climate, vegetation, soil properties and nutrient cycling leading to differences in SOM dynamics. The large amounts of labile SOM present in these soils, in combination with the results from our parallel studies of the temperature response kinetics of respiration (Sjögersten & Wookey, 2002), clearly indicate that a highly labile SOM pool is present in both tundra, and forest soils, and that temperature-related increases in CO_2 efflux can be maintained for at least 3 years. It is, however, still uncertain how different SOM fractions will respond to climate warming (Davidson *et al.*, 2000). Further, we have observed acclimatisation of soil respiration in response to higher soil temperature (Sjögersten & Wookey, 2002), which was also noted in US grassland prairie (Luo *et al.*, 2001). In our study, no significant effect of the OTCs on soil chemical properties was detected after 2 years of experimental warming, which is almost certainly due to the relatively short-term experiment in combination with the minor impact of the OTCs on soil temperature. The latter may be related to decreased soil moisture in the OTCs as well as to improved insulation due to increased canopy development of dwarf shrubs (R. Baxter, unpublished data) and suggests that the soil system is rather resilient to surface warming. However, given suitable conditions (i.e. improved availability of thermal energy and moisture) large amounts of soil C (*N-alkyls*, *O-alkyls* and acetals), especially in tundra soils, are potentially readily degradable by soil microorganisms. Our data therefore support the hypothesis that long-term climate warming involving shifts in the tree-line will increase the emission of CO_2 from mesic subarctic/arctic soils until a new quasi-equilibrium is established with the altered quantity and/or quality of litter inputs (Lloyd & Taylor, 1994; Peterjohn *et al.*, 1994; Wüthrich *et al.*, 1994; Kirschbaum, 1995; Simmons *et al.*, 1996; Nakane *et al.*, 1997; Bowden *et al.*, 1998; Londo *et al.*, 1999; Fang & Moncrieff, 2001; Illeris, 2001 (PhD thesis); Sjögersten & Wookey, 2002).

We focused on the organic soil horizon where most organic C is stored in these soils. The organic horizons also contain the most labile and temperature-sensitive SOM, which will be least protected from decomposition by association with clay particles and therefore will be the most susceptible to climate warming (Schimel *et al.*, 1996; Liski *et al.*, 1999). However, additional information on C chemistry at greater depth is required to provide a more comprehensive understanding of the dynamics of soil C in high latitude regions. At our Abisko sites, for example, ca. 30% of the surface soil respiration (measured at the surface) likely originates from decomposition of C in the mineral soil horizons (P. Thermaenius, pers. comm.).

To our knowledge, this is the first regional study of soil C composition analysed by CPMAS ^{13}C NMR in the Fennoscandian mountain range. Our results suggest that care must be taken when modelling C fluxes in this ecotone region, and that more detailed understanding of the underlying processes controlling the magnitude and nature of the decomposition processes are needed. Our study clearly demonstrates the need for long-term experiments, during which slow processes such as soil formation can be assessed in detail and the sensitivity of the system in relation to climate warming can be evaluated.

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